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Archaeogenomic insights into the adaptation of plants to the human environment: pushing plant–hominin co-evolution back to the Pliocene



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ABSTRACT

The colonization of the human environment by plants, and the consequent evolution of domesticated forms is increasingly being viewed as a co-evolutionary plant–human process that occurred over a long time period, with evidence for the co-evolutionary relationship between plants and humans reaching ever deeper into the hominin past. This developing view is characterized by a change in emphasis on the drivers of evolution in the case of plants. Rather than individual species being passive recipients of artificial selection pressures and ultimately becoming domesticates, entire plant communities adapted to the human environment. This evolutionary scenario leads to systems level genetic expectations from models that can be explored through ancient DNA and Next Generation Sequencing approaches. Emerging evidence suggests that domesticated genomes fit well with these expectations, with periods of stable complex evolution characterized by large amounts of change associated with relatively small selective value, punctuated by periods in which changes in one-half of the plant–hominin relationship cause rapid, low-complexity adaptation in the other. A corollary of a single plant–hominin co-evolutionary process is that clues about the initiation of the domestication process may well lie deep within the hominin lineage.

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Introduction

The exploitation of plants by humans is often viewed as a process of human dominance over plants that resulted in the domestication of many species. Such a perspective invokes a notion of passivity on the part of the plants, which may be considered to some extent ‘victims’ of the domestication process. Theorists have long considered the evolution of plant domestication to be a co-evolutionary process between plants and humans, in which both partners have become modified (Rindos, 1984; Harris and Hillman, 1989). Recently, evidence has accrued that this co-evolutionary process is one that stretches far further back in time than the

profusion of domestications that litter the late Pleistocene and early Holocene epochs.

The plant–hominin co-evolutionary continuum

The profound influence between plants and humans is apparent deep into the palaeoanthropological record. Plants adapted to the gradual cooling environment of the Neogene with the rise of many C4 lineages in parallel (Christin et al., 2011; Sage et al., 2011), with the grasses in particular predisposed to C4 evolution (Christin et al., 2013). The expansion of C4-dominated savannahs during the cooling latter stages of the Pliocene 2.8–2.4 mya (millions of years ago) is associated with an increase in the consumption of C4 foods in the diet of hominins such as *Australopithecus afarensis*, reflecting a greater dependence on warm season grasses and sedges as well as C4-grazing animals (Sponheimer and Lee-Thorp, 1999; Sponheimer

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et al., 2005, 2013; Lee-Thorp et al., 2010; Wynn et al., 2013; Cerling et al., 2013a, b). Whether this shift involved an increase in the direct exploitation of plants is still unknown, but the dietary shift of the time has been associated with major episodes in brain and digestive evolution in the genus *Homo* (Aiello and Wheeler, 1995). The hominin lineage departs from the rest of the hominids in part with a change in the interaction with plants. The increased use of stone tools enabled access to richer carbohydrate sources through both retrieval and processing, for instance through digging up roots, which led to a wider spectrum of plant species utilized (Hillman and Wollstonecroft, 2014).

A quickening of the direct interaction between hominins and plants is apparent at 100 kya (thousands of years ago), with grass seed consumption by early *Homo sapiens* in Mozambique (Mercader, 2009). Later evidence comes from Neanderthals up to 50 kya where plant material enshrined in the calculus matrix of teeth shows the consumption of plants later associated with domestication, such as *Hordeum*, *Phoenix*, and members of the Faboideae (Henry et al., 2011, 2014). Furthermore, an insight into the sophistication of this plant use is evident from the occurrence of starch granules showing damage that may be consistent with cooking. This 'early' starch economy is also apparent from the late Pleistocene (13.7–15.0 kya) of modern humans from dental caries and a broad range of plant materials from the same context, including grasses, oak, legumes, pines, and pistachio (Humphrey et al., 2014).

Around 10 kya, a large number of domesticated plants emerged, characterized by a common group of traits collectively termed the domestication syndrome (Harlan et al., 1973; Hammer, 1984). The basis of this emergence has been the subject of extensive debate (Brown et al., 2009; Larson et al., 2014). Originally described as a 'revolution' (Childe, 1928), it has become apparent that these domesticated forms of plants appeared at different times in different places (Fuller et al., 2011) and became modified with domestication syndrome traits at a pace that is more consistent with natural selection than strong artificial selection (Purugganan and Fuller, 2011).

The deep history of plant–hominin interaction and the parallel and relatively gradual appearance of domesticated forms suggest that the transition of plants to domesticated forms was part of the continuum. The amelioration of climate in the late Pleistocene saw the stabilization of human niche constructs (Smith, 2007; Laland et al., 2010) facilitated by (and facilitating) activities such as cultivation of wild plant communities. Evidence is now accruing that rather than a narrowly directed artificial selection of specifically targeted species, the evolutionary trajectory of domestication is better described as an outcome of plant communities actively adapting to a human niche construct.

The adaptation of plant communities to the human environment

The emergent human environment at the end of the last glaciation led to the evolution of both domesticated and commensal species. The domestication syndrome of traits that proved to be of adaptive value to plants included the loss of natural seed and fruit dispersal, changes in seed size, increased physical and chemical palatability, loss of sensitivity to environmental cues such as photoperiod, and changes in plant architecture (Fuller, 2007). The view from the archaeological record has developed in recent years from an apparently rapid appearance of domesticated forms of crops to a hitherto unappreciated long period of pre-domestication cultivation that stretched thousands of years back into the Pleistocene (Weiss et al., 2006; Willcox and Stordeur, 2012), and a slow subsequent fixation of traits over a period of thousands of years (Tanno and Willcox, 2006).

However, it was not only plants that were exploited for food that were involved in this adaptation to live within the human environment. Other small-seeded grasses and legumes also adapted and developed domestication syndrome traits such as non-shattering and an annual habit (Spahillari et al., 1999; Senda et al., 2006; Howard et al., 2011). Therefore, a community of plants that encompassed a range beyond that which could credibly be attributed to human choice thrived in the human environment.

The human environment to which the plant communities adapted was dynamic, presenting plants with new challenges leading to new adaptations, such as with the evolution of changing agrarian practices (Fuller et al., 2010). Consequently, the syndrome adaptations of the members of this community emerged in a staggered fashion in response to different selection pressures that appeared dynamically as the human environment developed (Fuller, 2007). The changing nature of the human environment resulted in a turnover of winners and losers among domesticated species (Conolly et al., 2008). The expansion of the human environment out of centers of domestication into new latitudes then presented plant communities with acute adaptive challenges. For plants, the environment changed in terms of temperature, rainfall, and day length, particularly in Europe and Asia as crops were dispersed northwards, and also in the Americas as Neotropical crops such as maize colonized temperate zones. The dynamic nature of this co-evolutionary relationship is evident from the later crossover of some commensals to domesticated forms, such as rye that was well-adapted to northern climes (Küster, 2000).

An important emergent aspect is that domesticated plant species appear to have adapted to their community composition rather than individually as separate domesticates that could function in isolation. It is possible that some features of the domestication syndrome itself could represent the consequences of internal competition between the community species. Consequently, cultural complexes as a whole appear to have been adapted to specific ecological niches (Banks et al., 2013). Hiatuses in the spread of the human environment to new latitudes are associated not only with the time required for the adaptation of crops to new physical environments, but crucially also for the adaptation to the changing composition of the agrarian package itself (Colledge et al., 2005; Coward et al., 2008).

The challenge of understanding how plant community systems became adapted to the human environment

A new framework to understand the evolution of domestication is emerging, one in which plants adapted as a community to the human environment rather than being the passive recipients of precision targeting of individual species by humans. The latter could be considered as isolated cases. Understanding how this adaptation occurred presents a major challenge, requiring approaches that consider systems level analyses, both at the community and genetic levels (Allaby, 2010; Kitchen and Allaby, 2013).

Adaptation through natural selection rarely involves a single gene. While some traits may be monogenic, such as loss of seed shattering in many cases, at any given time multiple traits are likely to be under selection. It may be tempting to regard these as independent processes, especially if the traits under consideration do not appear to be directly related. For instance, there is no expectation that seed shattering and seed size should be either controlled by overlapping genetic loci, or be traits that respond to the same environmental pressures. Although each locus under selection across a genome can be considered to involve a separate process, in reality there is a constraint on the limits of selection that can be endured. First identified and described by Haldane (1957), the cost of selection principle bridges the latter stages of the Modern

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